

The Mammals of the Ardis Local Fauna  
(Late Pleistocene), Harleyville, South Carolina

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**ABSTRACT**—The Ardis local fauna is contained within sediment-filled solution cavities of late Pleistocene age, located in the Giant Cement Quarry near Harleyville, Dorchester County, South Carolina. This paper, the second on the fossil remains collected from the Ardis site, documents 43 taxa of mammals recovered from a group of interconnected solution cavities, including 24 taxa of mammals not previously reported as fossils from the state. Fossil remains from the lowermost layers and the extreme upper layer of the deposit were  $C^{14}$  dated at  $18,940 \pm 760$  and  $18,530 \pm 725$  y.b.p., respectively, and are considered contemporaneous. Fossil remains were deposited near the height of the Wisconsin glaciation and appear to reflect a mosaic edge community, probably a patchwork of mixed hardwood and conifer forest, interspersed with meadows, possibly associated with a marsh or bog, located near a permanent stream or a river. The Ardis local fauna is composed of a mammal community which has no modern analogues ("disharmonious fauna"), and reflects a more equitable climate, cooler summers and warmer winters, than that presently occurring in the region.

## INTRODUCTION AND GEOLOGY

As collections of fossils continue to be amassed from various localities in South Carolina, the fossil record of the state likely will be one of the richest in the eastern United States. Long known as a source of marine mammal fossils of Eocene and Oligocene age, the State has a large number of vertebrate faunas from various other time periods. Although the Pleistocene epoch is one of the best represented in South Carolina, only two assemblages (Allen 1926, Roth and Laerm 1980) have been reported in the literature to date.

Our purpose is to present data on a collection of late Rancholabrean mammals, the Ardis local fauna (Appendix 1), found in the Giant

Cement Plant pit near Harleyville, South Carolina. This is the second (Bentley and Knight 1993) in a series of papers that reports the various taxonomic assemblages collected from this site.

The Giant Cement Plant, located about 5 km north-northeast of Harleyville, South Carolina (Fig. 1), is in Dorchester County, about 1 km from Interstate 26 at the Harleyville exit ( $33^{\circ}14'N, 80^{\circ}26'W$ ). It is a large, open-pit mine, in operation for the past 45 years. The stratigraphic assignments for the large exposures of middle Eocene Santee Limestone, which is exploited for cement products, were determined by Sanders (1974), who discussed the marine vertebrate and invertebrate material collected from the pit. Based on reports from Cooke and MacNeil (1952) and Malde (1959), Sanders (1974) refers to the layer which



Fig.1. Location of the Ardis local fauna.

unconformably overlies the Santee Limestone as the "Cooper Marl" of early to late Oligocene age. A more recent survey by Ward et al. (1979) recognizes three members of the "Cooper Marl" (Cooper Formation), the Ashley (Oligocene), the Harleyville (late Eocene), and the Parkers Ferry (late Eocene). The Parkers Ferry and Ashley members were absent at the Ardis fossil locality. Harris and Zullo (1991) refer to the Harleyville member as the Harleyville Formation, and we follow that practice in this paper. Since Sanders' (1974) study, fossil vertebrates of presumed late Pleistocene origin have been collected by workman and hobby collectors from several areas of the quarry, although no stratigraphic assignment could be determined for these fossils. Most were collected from spoil piles of unknown origin.

In April 1991, during a periodic visit to the quarry, the senior author, accompanied by Mr. Vance McCollum, a hobby collector, discovered a newly-mined area in the southeastern wall of the quarry which contained a dense concentration of late Pleistocene terrestrial vertebrate fossils. Giant Cement, in anticipation of further mining operations, had used a dragline to remove overburden from the underlying Santee Limestone. This was done in a single strip which formed a trench at a right angle in the southernmost corner of the pit. This tract of freshly mined earth had a maximum length of about 150 m, a width of 10 m, and a depth of 4 m. Fossils were initially collected from a single row of spoil piles dumped adjacent to the area from which they were mined. We determined that the fossil material came from a series of localized, sediment-filled cavities formed in the underlying Harleyville Formation and Santee Limestone. Groundwater had preferentially dissolved away the upper portions of the Santee Limestone, so that many of the solution cavities contacted the overlying, clay-rich Harleyville Formation. This resulted in the occasional collapse of the Harleyville Formation, opening several of the cavities to the surface.

The diameter of the solution cavities varied from a few centimeters to a maximum diameter of nearly 2.0 m, with many of the cavities interconnected. The solution cavities reached a maximum depth below the Harleyville Formation of about 4 m. The majority of the cavities were infilled with clastic sediment from the surface. The sediment is well stratified and ranges in size from clay to small pebbles. Multiple fining-upward sequences within the cavity-filling deposits indicate episodic sedimentation, perhaps corresponding to flood events within a nearby fluvial system. The undisturbed clay layers within the cavity-filling and the narrow interconnecting nature of the cavities indicate that the entire deposition probably occurred over a relatively short time

span. This tends to be confirmed by the limited range of carbon dates. The Harleyville Formation was capped by a well sorted, cross-stratified quartz sand having a maximum thickness of about 4 m. Fossils collected from this layer were similar to those in the cavities, but fewer in number.

Locally, several cavities which had no connections to the surface were exposed by mining operations in the Santee Limestone. Consequently, these cavities were not infilled from above.

A systematic excavation was not possible because the area at the time of discovery was actively being mined. The operators of the mine graciously relocated their mining operation to another section of the pit, allowing us the maximum possible study time and nearly unlimited access to the fossil deposit. Bert Ardis, an employee of the Giant Cement Plant Company, played a crucial role in the discovery and excavation of fossils from the quarry. In recognition of his efforts the fauna was named in his honor.

#### DATING OF THE DEPOSIT

Kruger Enterprises, Inc., Cambridge, Massachusetts, used  $C^{14}$  dated ( $C^{13}$  corrected) mammal and reptile bone apatite to date fossil materials from the lower levels of the solution cavities and from the well-sorted sand layer above the Harleyville Formation. Dating was done on apatite due to the paucity of collagen. The fossil material from the solution cavities (300 g of mixed mammal and reptile bone) were dated at  $18,940 \pm 760$  y.b.p. and the fossil material (300 g of mammoth bone), from the overlying unnamed, quartz sand layer (about 1 km from the primary deposit), dated at  $18,530 \pm 725$  y.b.p. The overlap of the two dates suggests that the material in the solution tunnels and the homogeneous sand layer above the Harleyville Formation are contemporaneous. These dates place the time of deposition at, or near, the height of the Wisconsin glaciation (Bowen 1988).

Serious questions have recently been raised concerning the reliability of  $C^{14}$  dating based on bone apatite and collagen (Stafford et al. 1991). They state that  $C^{14}$  dates on noncollagenous bone may yield dates potentially thousands of years too young. Efforts are underway to acquire an amino acid date, even though the apatite sample was apparently very clean (Kruger Enterprises, Inc., personal communication). In light of recent work (Stafford et al. 1991), the  $C^{14}$  dates we used will be considered a minimal age for this deposit. The maximum age of the deposit is not expected to exceed 22,000 y.b.p. (Kruger Enterprises, Inc., personal communication). Whatever the date, however, there is little doubt that the fauna represents a late Rancholabrean age, and minor revisions in the absolute dates would have little effect on the ecological or climatic interpretations suggested in our paper.



## METHODS

All fossil material reported here was collected during periodic trips into the quarry by the authors and a group of volunteers. We collected fossil material from the surface of associated spoil piles as well as by screen sifting the fossiliferous sand. Screens used were 20 gauge (1.0 mm) to quarter-inch (6.35 mm) mesh. Materials in situ were collected by a combination of screen-washing and by applying a gentle, controlled stream of water to the exposed sands. Fossils were exposed as the sand was gently washed away.

Most specimens from the Ardis local fauna were deposited in the South Carolina State Museum collections and are registered under the accession base number of S.C. 93.105. We cite such specimens in this paper only by the numbers following that base number. Fossils that were accessioned separately in the South Carolina State Museum's collections will be designated by S.C. followed by five to six digits. Fossil specimens deposited in the National Museum of Natural History have been accessioned under the number of 407498 and are indicated by an institutional prefix of USNM in the text. Fossil material deposited at the Florida Museum of Natural History will be referred to by an institutional prefix of UF.

Taxonomy for extant and extinct taxa follows Wilson and Reeder (1993) and Kurten and Anderson (1980), respectively. Common names were taken from Webster et al. (1985), and Kurten and Anderson (1980). Under Materials, capital "M" denotes upper dentition, lower case "m" denotes lower dentition.

## SYSTEMATICS

Class Mammalia

Order Didelphimorphia

Family Didelphidae

*Didelphis virginiana* - Virginia Opossum

Material: 1 left dentary with m1 and m2 and an unerupted p3 (.1); 1 left dentary with m2 and m3 (.2); 1 left maxilla fragment with P3 and M1 (.3); 1 right M3 (.8); 1 right M1 (.9); 6 right partial dentaries (3 USNM & 3 UF); 1 left dentary, proximal one third (USNM); 1 right proximal dentary fragment (USNM); 4 left humeri, distal ends (.4-.7).

Remarks: The opossum is found throughout most of the United States and northward into Canada. Late Pleistocene fossils are restricted to the southern parts of the United States, and the species is believed to have radiated into the northern part of the continent during historical times (Kurten and Anderson 1980). The species is common today in the vicinity of the Ardis locality.

This is the first published report of fossil *D. virginiana* from South Carolina.

Order Xenarthra  
Family Megalonychidae  
*Megalonyx jeffersoni* - Jefferson's Ground Sloth

Material: 1 upper right 3rd molariform (.194).

Remarks: This sloth has been found as far north as Canada and the western coast of Alaska, and formerly ranged throughout the United States except for the Rocky Mountains, Great Basin, and the arid or desert areas of the Southwest. It is thought that the diet of this sloth consisted of twigs and leaves and that it inhabited forested or wooded areas (Kurten and Anderson 1980).

Previous reports of this species from South Carolina include Hay (1923) and material from Edisto Island (Roth and Laerm 1980).

Family Dasypodidae  
*Dasypus bellus* - Beautiful Armadillo

Material: 25 buckler osteoderms (.200- .210), (5 USNM), (9 UF); 11 movable osteoderms (.195- .199), (3 USNM), (3 UF); 1 cephalic osteoderm (.211); 1 caudal vertebra (.212).

Remarks: This armadillo probably fed primarily on insects and that diet might have restricted its range to moderate climes (Kurten and Anderson 1980). However, Voorhies (1987) questioned its reliability as a warm weather indicator. Its occurrence with mostly boreal forms in the Craigmile local fauna, Nebraska (Rhodes 1984), suggests that it may have been able to withstand weather conditions considerably cooler than *D. novemcinctus*. *D. bellus* fossil records are well established in South America and the southern portions of the United States (Kurten and Anderson 1980). This suggests that *D. bellus* is a fairly reliable indicator of warm climates, and the material from Nebraska may represent a fringe population. Although a common Pleistocene fossil, this is only the second report of this species from South Carolina. It was first reported by Roth and Laerm (1980) from Edisto Island.

Family Pampatheriidae  
*Holmesina septentrionalis* - Northern Pampathere

Material: 1 partial buckler osteoderm (.227); 1 cephalic osteoderm (.228).

Remarks: Differentiation of the cephalic and buckler osteoderm was based on the descriptions of Edmund (1985).

Little is known about its diet, which probably consisted of coarse vegetation (based on large, flat, high-crowned teeth of indeterminate growth). Regarding its habitat, *Holmesina* is suspected to be intolerant of cold climates (Kurten and Anderson 1980).

*Holmesina* was first reported from South Carolina by Roth and Laerm (1980) at Edisto Island.

Order Insectivora

Family Soricidae

*Blarina brevicauda* - Northern Short-tailed Shrew

Material: 2 right maxillae with the M1 and M2 (.11, .12); 4 right dentaries with m2 and m3 (USNM); c1, p1, p2, m1, m2 (.13); c1, m1 (.14); c1, p1, p2, m1 (.15), respectively; 2 left maxillae with M1, M2, M3 (.16) and M1 (.17) respectively; 1 left dentary with m1-m3 (.18); 1 isolated c1 (.19).

Remarks: Identification was made on the basis of characters listed by Guilday (1962) and by direct comparisons to fossil and recent specimens. Ardis specimens are indistinguishable from modern comparative materials of *B. brevicauda* and are generally larger in size than samples of *B. carolinensis* (Graham and Semken 1976). Apparently *B. brevicauda* size reflects a positive Bergmann's response, suggesting that the fossils from the Ardis site are a more northerly stock and not the smaller southern species *B. carolinensis* (McNab 1971, Guilday et al. 1977, Klippel and Parmalee 1982, Jones et al. 1984).

The northern short-tailed shrew occurs in a variety of terrestrial habitats from forests, fields and meadows, to salt marshes. Today this species occurs, in South Carolina, only in the extreme northwestern portion of the State, nearly 300 km from the fossil locality. An isolated population on the coast of North Carolina is about the same distance from the site (Webster et al. 1985). *B. carolinensis* does occur in the area of the Ardis site today.

This is the first fossil record of *B. brevicauda* reported from South Carolina.

*Sorex* sp. cf. *S. longirostris* - Southeastern Shrew

Material: 1 left dentary with complete dentition (.10).

Remarks: Guilday (1962) and Guilday et al. (1969, 1977) separated *Sorex cinereus* from *S. longirostris* based on a slightly larger mean size of *S. cinereus*, because tooth morphology is nearly identical. The

P4-M3 measurement of our specimen (3.64 mm) fell at the bottom of the range for *S. cinereus* and below the mean given for that species at both New Paris Cave No.4, Pennsylvania, and Clark's Cave, Virginia (Guilday 1964, Guilday et al. 1977). Because the Ardis local fauna contains many extralimital species, both northern and southern, and because of the morphological ambiguity between *S. longirostris* and *S. cinereus* (Jones et al. 1991), the fossil specimen from the Ardis site is tentatively assigned to *S. longirostris* and not *S. cinereus*, as only the former occurs in the area of the Ardis site today. The *Sorex longirostris* P4-M3 measurement is considerably larger than that of *S. hoyi* (Guilday et al. 1977).

At present the southeastern shrew ranges from southeastern Arkansas, east to central Florida, and north along the Atlantic coast into Maryland. It is associated with moist, open fields and lowland forests but can also be found in dry upland fields (Webster et al. 1985). In the late Pleistocene this shrew has been reported only from the late Rancholabrean Haile 11B and Arredondo sites in northern Florida (Kurten and Anderson 1980, Webb and Wilkins 1984). The Ardis site is the first identification of this shrew from the Wisconsin time period and from South Carolina.

#### Family Talpidae

##### *Condylura cristata* - Star-nosed Mole

Material: 3 humeri (.20-.22).

Remarks: Identification was made by comparisons to recent specimens. Humeri of this species differ from those of *S. aquaticus* in having a less robust humeral shaft and a smaller width at both proximal and distal ends.

At present *C. cristata* occurs in the upland and the Coastal Plain of South Carolina but is absent from the midland area. The star-nosed mole is an excellent swimmer and inhabits areas that have moist soils or are located near water (Webster et al. 1985). It may be found in wooded areas, meadows or fields, swamps, and bogs. Today, it is found in the area of the Ardis site.

This is the first fossil report of this mole from South Carolina.

##### *Scalopus aquaticus* - Eastern Mole

Material: 16 humeri (.23-.26), (6 USNM), (6 UF).

Remarks: These humeri are separated from other South Carolina mole species on the basis of their greater robustness, which may reflect a more fossorial life style.



The eastern mole ranges from the eastern to midwestern United States, commonly inhabiting well-drained sand or loam soil types, and less common in clay or gravel soils (Webster et al. 1985). Eastern moles are found today in the vicinity of the fossil site.

This is the first fossil record of this species for South Carolina.

Order Carnivora

Family Canidae

*Urocyon* sp. cf. *U. cinereoargenteus* - Gray Fox

Material: 1 metapodial (.254).

Remarks: Felid metapodial elements are generally more robust and have a more acute curvature to the shaft in comparison to modern canid specimens in the Florida Museum of Natural History collections (Gary Morgan, Florida Museum of Natural History, personal communication). The proximal articulation varies significantly from all felids examined and most closely parallels those of canids. The curvature of the elongated shaft, overall size, and simple articulations of the proximal end suggest a close affinity to *U. cinereoargenteus*. A small convexity dorsal and anterior to the proximal articulation was the most significant variation between the fossil element and recent specimens of the gray fox.

Roth and Laerm (1980) refer an Edisto Beach ulnar fragment to this species but state that it may be recent.

*Canis dirus* - Dire Wolf

Material: 1 brain case (SC 91.171.1); 1 left c1 (.251); 1 metapodial shaft (.252); 1 left jugal (.253).

Remarks: The dire wolf is one of the more common late Pleistocene canids recovered from North American fossil sites (Kurten and Anderson 1980). The material recovered from the Ardis site is believed to represent "wash-ins," as many of the elements, particularly the brain case, show signs of weathering and abrasions prior to fossilization. This represents the second reported occurrence of the dire wolf from this State, as *C. dirus* was reported from Edisto Island (Roth and Laerm 1980).

## Family Felidae

## Subfamily Machairodontinae

cf. *Smilodon fatalis*. - Sabertooth

Material: 1 left occipital condyle (.266).

Remarks: The shape and size of the condyle has its closest affinities with *Smilodon* and differs significantly from any other large mammal. The identification is extremely tenuous, however, and after an exhaustive search, represents the best possible solution to the identification of this specimen.

## Subfamily Felinae

*Lynx rufus* - Bobcat

Material: 1 right dentary lacking teeth, proximal end missing behind m3 alveoli (.267).

Remarks: This specimen is extremely similar to mandibles of *Lynx rufus* especially in general ramus shape, and alveolar count and placement. The bobcat inhabits a range of habitats including deserts, swamps, and upland forests (Kurten and Anderson 1980), and it occurs in the Ardis local fauna area today (Webster et al. 1985).

This is the first fossil record of *Lynx rufus* from South Carolina.

## Family Mustelidae

## Subfamily Lutrinae

*Lontra canadensis* - River Otter

Material: 1 cranium missing the right zygomatic arch and retaining only the left P1-M1 (SC 91.116.1); 1 atlas vertebra (.242); 1 caudal vertebra (.243).

Remarks: The river otter once occurred throughout the United States, including Alaska, but has been extirpated from many areas of the Midwest and Appalachian Highlands. The otter occurs sparsely throughout South Carolina, inhabiting a wide range of aquatic habitats. It appears to be most abundant in coastal estuaries and the lower reaches of rivers in the State (Webster et al. 1985).

This is the first fossil record of this taxon from South Carolina.

## Subfamily Mephitinae

*Spilogale putorius* - Eastern Spotted Skunk

Material: 1 proximal end of the right dentary with the alveoli for a partial m2 and for the m3 (.244).

Remarks: The partial dentary was differentiated from *Mustela vison* because the condyle tapers to a point lingually, whereas it is blunt in *Mustela vison*. The ramus of *Spilogale* is generally smaller and less robust, is laterally compressed, and lacks the distinct curvature found in mink. It also lacks the flattened ventral proximal edge found in the dentary of mink. It differed from other mustelids in the shape and size of the M2 alveoli and overall jaw size and shape. It is significantly smaller than skunks of the genera *Conepatus* and *Mephitis* and is most similar to *Spilogale* in size and general jaw morphology.

The eastern spotted skunk is found typically in prairies, brushy open forests, and mountain habitats. They no longer occur in the immediate area of the fossil site and are found sparsely in the Piedmont of South Carolina today (Webster et al. 1985).

This represents the first fossil record of this species from the State.

#### *Mephitis mephitis* - Striped Skunk

Material: 1 partial right dentary containing the alveoli of the m3 (.245); 1 left M1 (.256).

Remarks: The partial dentary was assigned to this species based on the length of the third molar and the presence of auxiliary roots. The overall size of the dentary was intermediate between *Spilogale* and *Conepatus*.

The striped skunk is found in the area of the site today and throughout much of North America and well into Central America (Hall 1981). It can be found in habitats varying from high mountain forests to brushy, semi-open areas, but appears to be much less common in wetlands (Webster et al. 1985).

This is the first report of the striped skunk in the fossil record from South Carolina.

#### *Conepatus* sp. cf. *C. robustus* - Extinct Hog-nosed Skunk

Material: 1 humerus (.247); 1 femur (.248); 1 partial dentary with p3 and alveoli of m1 (.249); 1 astragalus (.250).

Remarks: The fossil remains have been referred to this species based on their extremely large size in comparison with the living hog-nosed skunk *Conepatus leuconotus* (Martin 1978). The Ardis fossils exhibit a 30% size increase over *C. leuconotus*. No definable differences were observed between the Ardis material and the type of *C. robustus* from

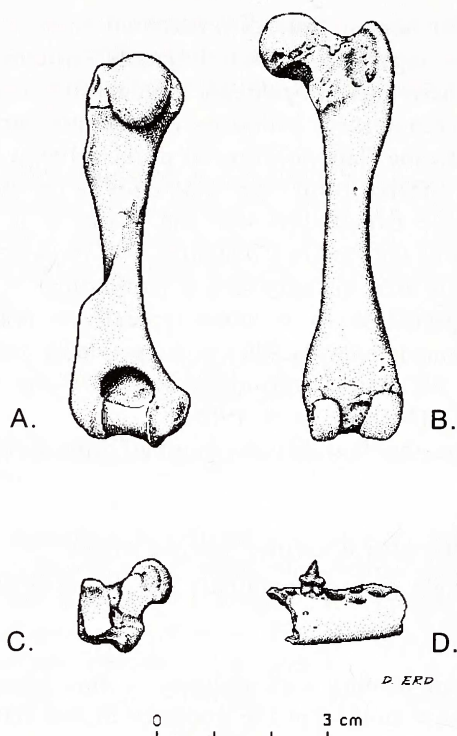


Fig. 2. *Conepatus* sp. cf. *C. robustus* material recovered from the Ardis local fauna. A) Humerus B) Femur C) Astragalus D) Dentary with p3.

the late Rancholabrean Haile 14 in Florida (Martin 1978). The femur and astragalus are the first of these elements to be reported for this species and were assigned based on morphology and their large size (Fig. 2). The extant species inhabit the southwestern United States, southward into Central America, and as far east as eastern Texas (Hall 1981).

This is the first report of this species from South Carolina and the first fossil record of this extinct hog-nosed skunk from outside of Florida.

#### Subfamily Mustelinae

#### *Mustela vison* - Mink

Material: 1 left dentary, complete dentition except for incisors (1 USNM); 1 left dentary, complete dentition except for incisors and



canine (.229); 1 partial maxilla with P3 and M1 and partial zygomatic arch (.231); 2 canines (.232, .233); 1 left dentary with p3 and m1 (.230); 1 left dentary with alveoli p2-m2 (.234); 1 left dentary (in the private collection of Lee Hudson, Florence, S.C.); 2 right ulnae (.235, .236); 1 thoracic vertebra (.237); 1 lumbar vertebra (.238); 1 right 3rd metatarsal (.239); 1 left 2nd metatarsal (.240); 1 rib (.241).

Remarks: Mink remains are generally uncommon in Pleistocene deposits (Kurten and Anderson 1980), but it was the most common carnivore at the Ardis site. This abundance might be explained by its relatively small size and ability to enter cavities that may have excluded larger carnivores. Mink may have also been attracted to favored prey items, in particular a large muskrat population which was using the cavities for various reasons. Muskrats are commonly fed upon by mink, and during certain times of the year, depending on availability, make up the bulk of their diet (Proulx et al. 1987). Mink are good indicators of nearby bodies of water and are found in a variety of habitats bordering water including rivers and streams, swamps, drainage ditches, marshes, and lakes (Webster et al. 1985). Mink are not abundant in South Carolina today, although they probably occur in the area of the Ardis site.

This is the first reported fossil record of this species from South Carolina.

Family Procyonidae  
Subfamily Procyoninae  
*Procyon lotor* - Raccoon

Material: 1 left dentary with m3 present and m1 alveoli (.255); 1 left dentary with p4-m2 alveoli (.256); 1 left m1 (.257); 1 right proximal end of dentary with m2 alveoli (.258); 1 left humerus shaft with partial distal end (.259); 1 left humerus distal end (.260); 1 right ulna proximal end (.261); 1 right humerus partial distal end (.263); 1 radius distal half (.262).

Remarks: The distribution of the raccoon is from Panama north through Mexico and the United States into the central portions of Canada (Hall 1981). Its habitat is ubiquitous, but is generally in or near forested wetlands such as stream and river bottoms, marshes, swamps, ponds, and lakes as well as upland and agricultural areas (Webster et al. 1985). Fossil remains of *P. lotor* are generally common in the United States during the late Pleistocene, especially in sinkhole and cave deposits (Kurten and Anderson 1980). The first South Carolina fossil of the raccoon was reported from Edisto Island (Roth and Laerm

1980), based on mandibular fragments and postcranial remains. The material from the Ardis local fauna represents the second report of fossil *P. lotor* from South Carolina.

#### Family Ursidae

##### *Tremarctos floridanus* - Florida Cave Bear

Material: 1 right m3 (.264); 1 first right metatarsal (.265)

Remarks: The m3 of *Tremarctos floridanus* differs from *Ursus americanus* in that it lacks the double root, and is substantially smaller than any other ursid in the eastern United States. The Florida cave bear has been recovered from Rancholabrean sites in Florida, Georgia, Tennessee, Kentucky, New Mexico, Texas, and northern Mexico (Kurten and Anderson 1980). Based on the fossil record it would appear that the Florida cave bear had a more southeastern distribution during the late Pleistocene. The material from the Ardis local fauna represents the second report of this species (Roth and Laerm 1980), from South Carolina. Both reports are from deposits along the Coastal Plain of the State.

#### Order Proboscidea

##### Family Mammutidae

##### *Mammut americanum* - American Mastodon

Material: 1 partial milk tooth (.332); 2 partial molars (.333, .334).

Remarks: The American mastodon was first reported in the fossil record for South Carolina from Edisto Island by Roth and Laerm (1980).

#### Family Elephantidae

##### *Mammuthus columbi* - Columbian Mammoth

Material: 1 complete molar (.335); partial molar (.336); partial scapula (in the collections of Lander University).

Remarks: All identifiable *Mammuthus* remains from the area of the Ardis local fauna have been recovered from the quartz sand layer above the Harleyville clay, and not in direct association with the Ardis fauna proper. Identification is based on the lamellar frequency (7) of the occlusal surface coupled with the late Pleistocene date of the site (Kurten and Anderson 1980). Carbon dating of the bone from a scapula associated with a complete and a partial molar of *M. columbi* gave a date of  $18,530 \pm 725$  y.p.b., within the range of the Ardis local fauna and here considered contemporaneous with it.

All other *Mammuthus* material reported previously from South Carolina has been assigned to *M. columbi* as well (Hay 1923, Allen 1926, Roth and Laerm 1980).

Order Proboscidea  
gen. et spec. indet.

Material: 1 distal fragment of tibia (.337); 1 vertebra (.340); 1 proximal rib end (.338); 6 fragments of ivory (.339a-c), (3 USNM).

Remarks: Identification to a particular family is not possible because of the fragmentary nature of these remains. Because the openings of the solution cavities to the surface were small, and large mammals are only represented by isolated fragments, these animals probably died on the surface nearby and were washed in by periodic flooding.

Order Perissodactyla  
Family Equidae

*Equus* cf *E. complicatus* - Complex-toothed Horse

Material: 2 partial incisors (2 USNM); 1 left M1 or M2 (1 USNM); 1 left DP3 or DP4 (.320); 1 right P3 or P4 (.319); 2 right M3s (1 USNM), (1 UF); 1 left m3 (1 USNM); 1 canine (.322); associated-1 axis, 3 caudal vertebrae, 1 incisor, and 3 rib fragments (.321a-h); 1 left distal radial end (.323); 1 right fourth metatarsal (.324); 1 left second metacarpal (.331); 2 left cuneiforms (.325, .326); 1 right magnum (.327); 1 right lunar (.328); 2 medial phalanx (.329, .330).

Remarks: The *Equus* cheek teeth from the Ardis local fauna have been tentatively assigned to the species *E. complicatus* based on the extremely complex nature of the occlusal surface. All other remains, because of the ambiguity in postcranial elements between *E. complicatus*, *E. fraternus*, and *E. occidentalis*, are referred to only as *Equus* sp.

Fossil remains assigned to the genus *Equus* were reported from South Carolina by Hay (1923), Allen (1926), and Roth and Laerm (1980).

Family Tapiridae  
*Tapirus veroensis* - Vero Tapir

Material: 1 partial right m3 (1 USNM); 1 partial m2 (UF); 2 partial left m3 (.316, .317); 1 partial right molar (.318).

Remarks: Tapir remains are among the more commonly collected Pleistocene fossils in South Carolina. Several tooth fragments referred to *T. haysii* were reported by Allen (1926) and represent the first record of tapir from South Carolina. Roth and Laerm (1980) reported numerous tooth fragments and some postcranial material from Edisto Island, but because of the fragmentary nature of the fossils, were unable to assign them to species. A virtually complete skull of *T. veroensis*, reported on by Ray and Sanders (1984), was collected by a diver in the Cooper River near Charleston, South Carolina. The material from the Ardis site is referred to *T. veroensis*, based on the generally smaller size of the molars in comparison to *T. haysii*. Extant species are semiaquatic browsers having a Neotropical distribution, with North American fossil localities suggesting a distribution south of glaciated areas during the Pleistocene (Kurten and Anderson 1980).

Order Artiodactyla

Family Tayassuidae

*Mylohyus nasutus* - Long-nosed Peccary

Material: 1 right dp2 (.306); 1 m1 or m2 (.307).

Remarks: This species, referred to as *M. pennsylvanicus*, was first reported from South Carolina by Allen (1926). Fossils from Edisto Island were referred to as *M. cf. M. fossilise* by Roth and Laerm (1980). Both names are synonyms of *Mylohyus nasutus*, following Kurten and Anderson (1980).

Family Camelidae

*Palaeolama mirifica* - Stout-legged Llama

Material: 1 partial lower molar (.268); 1 partial upper molar (.269); 1 left ectocuneiform (.270); 1 phalanx distal end (.271); 1 phalanx proximal two-thirds (.272); 1 hoof core (.273); 1 partial calcaneum (.274); 1 thoracic vertebra (.275); 1 metatarsal 3&4 proximal end (.276); 1 astragalus (.277).

Remarks: Identification was based on the presence of a weak "llama buttress" on the lower molar, and a weakly developed styloid (Webb 1974b), and a low crowned cheek tooth. Distinctive postcranial remains were compared directly to other camelid material.

It appears that the northern limits of this stout-legged llama were generally restricted to low temperate latitudes, e.g., southern California, the Gulf Coast of Texas, and Edisto Island, South Carolina (Roth and Laerm 1980), although it has been recorded in Missouri as



well. It is thought that the diet of this llama consisted of grasses as well as the shoots and leaves from bushes and trees (Kurten and Anderson 1980). The Ardis local fauna is the second report of this species from South Carolina.

Family Cervidae  
Subfamily Odocoileinae

*Odocoileus virginianus* - White-tailed Deer

Material: 1 left M1 (.278); 1 left m1 (1 USNM); 1 right M1 (.282); 1 right M1 (1 USNM); 1 left P3 (.279); 1 right p3 (1 UF); 1 right P1 (.283); 1 right m3 (.284); 1 left m2 (1 UF); 2 dm's (.280, .281); 1 left P2 (1 USNM); 1 right scapula proximal end (.285); 1 humerus distal end (.305); 1 distal end of calcaneum (.286); 1 astragalus (.287); 3 cubonavicular (.288, .289), (1 USNM); 1 right scaphoid (.290); 1 trapezoidomagnum (.304); 1 ectocuneiform (.315); 2 right proximal ulnas (.291, .292); 1 sacral vertebra (.293); 2 distal right radii (.294, .295) and 1 right radius of sub-adult (.296); 1 left proximal tibio-fibula (.297); 1 ulna partial proximal end (.298); right articulated (2) metatarsus and hoof core (.299a-c); 1 right metacarpal (.300); 1 right rib proximal end (.301) and 1 unspecified rib proximal end (.302); 1 right partial antler including the burr and past first two tines both of which are missing (1 USNM); 1 right antler (.303).

Remarks: The first fossil record of *O. virginianus* reported from South Carolina was based on two basal antler fragments (Allen 1926). A second record exists from Edisto Island (Roth and Laerm 1980), based on antler fragments and other postcranial remains, but these may be of recent origin. The white-tailed deer ranges from Canada into northern South America, but is absent from hot arid areas of North America. It occupies a wide variety of habitats today, including coniferous and deciduous forests, high mountain areas, coastal marshlands, grasslands, and suburban fringes. It is most commonly found in broken habitats typical of agricultural areas (Webster et al. 1985).

This deer is very common around the Ardis site today. The Ardis local fauna appears to have individuals from several different age cohorts, based on tooth wear patterns.

Family Bovidae  
Subfamily Bovinae  
*Bison antiquus*

Material: 1 right m2 (UF); 1 left P4 (.308); 1 left M2 (.309); 1 left p3 (.310); 1 left p2 (.311); 1 right M3 (USNM); 1 left m3 (.312); 2

lumbar vertebrae (.313), (USNM); 1 metacarpus (.401); 1 lunar scaphoid pisiform (.314); 1 neural process (USNM), 1 right hoof core (S.C. 92.22.1).

Remarks: Leidy (1860) reported the first bison material from South Carolina, as *B. latifrons*. Hay (1923) mentions a fossil which he refers to as *Bison* sp., and Allen (1926) identified a single molar as *Bison* sp. cf. *B. bison*. Allen also mentions a horn core and suggests that it belongs to a bovid. The Edisto Island fossil assemblage (Roth and Laerm 1980) contains bison material and is identified only as *Bison* sp. The molars and postcranial material from the Ardis site are assigned to *B. antiquus* based on size. These specimens are larger than modern *B. bison* and comparable in size to *B. antiquus*.

This is the first report of *Bison antiquus* from South Carolina.

Order Rodentia  
Family Sciuridae

*Glaucomys volans* - Southern Flying Squirrel

Material: 1 left femur (.171).

Remarks: The specimen, a femur broken just below the distal end, is assigned to *G. volans* based on the length of the shaft compared to the width of the proximal end, and overall smaller size compared to *G. sabrinus*.

This species is found commonly today in the eastern United States. It ranges as far north as Canada and southwest into Mexico and Guatemala (Kurten and Anderson 1980).

Typical habitats are deciduous and mixed hardwood forests. *Glaucomys* fossils found in the southeastern United States are commonly collected from cave deposits frequented by birds of prey during the time of deposition (Guilday 1962; Guilday et al. 1969, 1977, 1978; Grady and Garton 1982). The femur is believed either to have been "washed in" or carried by a non-avian predator. There is no evidence of regurgitated pellets from roosting raptors, and the entrances and the chambers of the solution tunnels throughout the site were too small to facilitate large roosting birds.

This represents the first fossil evidence of a southern flying squirrel in South Carolina.

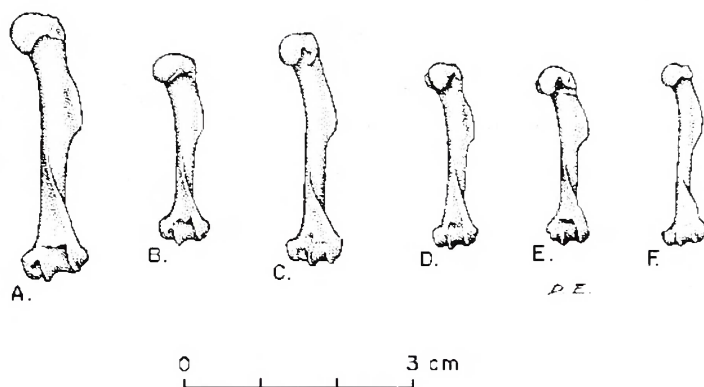


Fig. 3. Comparisons of recent squirrel humeri to the Ardis fossil specimen. A) *Spermophilus franklini* (USNM-54153) B) *Spermophilus lateralis* (USNM-250744) C) *Tamiasciurus hudsonicus* (USNM-505592) D) *Spermophilus tridecemlineatus* (USNM-255383) E) *Spermophilus tridecemlineatus* Ardis local fauna (.175) F) *Tamias striatus* (USNM-347965).

#### *Sciurus carolinensis* - Gray Squirrel

Material: 1 right humerus proximal half (.172); 1 right tibia proximal half (.173); 1 left tibia distal one third (.174).

Remarks: The material is distinguished from *Sciurus niger* by its smaller size and is indistinguishable from recent material of the gray squirrel. This species ranges throughout the eastern half of the United States north into Canada, where it inhabits deciduous and coniferous forests, timbered streams, and bottomlands (Webster et al. 1985).

This is the first fossil record of the gray squirrel from South Carolina.

#### *Spermophilus tridecemlineatus* - Thirteen-lined Ground Squirrel

Material: 1 left humerus (.175).

Remarks: In comparisons with recent humeri of mustelids, microtines, cricetids, and a variety of ground squirrels, all others were eliminated because of various morphological inconsistencies. *Tamias striatus* humeri vary significantly from *S. tridecemlineatus* with differently shaped proximal condyles and distal articulations. The humeral shaft is noticeably more slender with respect to the total length in *Tamias striatus* than in *S. tridecemlineatus*. *Tamiasciurus hudsonicus* humeri have a

broader distal end and are considerably larger than *S. tridecemlineatus*. The humerus of *S. franklinii* is significantly larger (2x) and varies morphologically from *S. tridecemlineatus*. The fossil humerus is indistinguishable from that of *Spermophilus tridecemlineatus* and given geographical and temporal considerations is assigned to this species (Fig. 3).

The thirteen-lined ground squirrel has a modern range reaching into central Canada, south into eastern Utah and central Texas, and eastward through the Midwest into Ohio (Hall 1981). The fossil specimen from the Ardis site is about 1,000 km southeast of its present day distribution. *S. tridecemlineatus* inhabits shortgrass prairies and does not occur in forested areas (Kurten and Anderson 1980). Clark's Cave and Natural Chimneys, Virginia, and Baker Bluff Cave, eastern Tennessee, are the closest fossil localities containing remains of *S. tridecemlineatus*. Martin and Webb (1974) reported *Spermophilus* sp. from Haile 14A in Florida, which is the most southeastern report of this genus. This ground squirrel's presence in the East has been interpreted as indicating parkland or semi-prairie conditions (Guilday et al. 1977, Kurten and Anderson 1980).

This is the first fossil record of *Spermophilus tridecemlineatus* from South Carolina.

#### Family Castoridae

##### *Castor canadensis* - Beaver

Material: 1 left M3 (.176); 1 partial incisor (.177); 1 left M2 (.178); 1 radius (.180); 1 tibio-fibula distal end (.179); 1 metatarsal (.193); 1 phalanx (.181); 1 thoracic vertebra (.182); 1 caudal vertebra (.183).

Remarks: The beaver is found throughout most of North America except for southern peninsular Florida, the arid regions in the Southwest, and along Arctic shorelines (Kurten and Anderson 1980). The presence of this semiaquatic species in the Ardis local fauna indicates the presence of a nearby wooded, permanent body of water.

Presence in the South Carolina fossil record from Edisto Beach was first established by Roth and Laerm (1980), although they state that the single postcranial element may be modern.

#### Family Muridae

##### Subfamily Arvicolinae

##### *Ondatra zibethicus* - Muskrat

Material: 1 complete skull (.27); 2 partial skulls (1 USNM), (1 UF); 4 parietals (.28-.30), (1 USNM); both maxillaries and palate missing



only left M1 (.31); 9 right dentaries (.32-.35), (3 USNM), (2 UF); 8 left dentaries (.36-.38), (2 USNM), (3 UF); 1 left m1 (.39); 1 left m2 (.40); 1 right m2 (.41); 1 right m3 (.49); 1 left m3 (.50); 4 right M1 (.47, .48), (2 USNM); 4 left M1 (.42-.45); 1 right M3 (.46), 1 left M3 (.39); 1 left and 1 right lower incisor (.51, .52); 1 upper left incisor (.53); 12 left femora (.54-.59), (3 USNM), (3 UF); 10 right femora (.60-.63), (3 USNM), (3 UF); 9 left humeri (.64- .66), (3 USNM), (3 UF); 3 right humeri (.67- .69); 12 left tibio-fibula (.70-.75), (3 USNM), (3 UF); 13 right tibio-fibula (.76- .82), (3 USNM), (3 UF); 8 left ulna (.83-.86), (2 USNM), (2 UF); 9 right ulna (.87-.89), (3 USNM), (3 UF); 2 radii (.90- .91); 1 partial ilium (.92); 11 left partial innominates (.93- .97), (3 USNM), (3 UF); 11 right partial innominates (.98-.104), (2 USNM), (2 UF); 2 left 1st metatarsals (.105, .106); 2 left 2nd metatarsals (.121, .122); 3 left 3rd metatarsals (.115-.117); 3 right 1st metatarsals (.118- .120); 7 right 2nd metatarsals (.107- .109), (2 USNM), (2 UF); 5 right 3rd metatarsals (.110- .112), (1 USNM), (1 UF); 2 right 4th metatarsals (.113, .114); 3 calcanea (.123- .125); 1 atlas vertebra (.126); 2 axis vertebra (.127, .128); 1 3rd cervical vertebra (.129); 2 5th cervical vertebrae (.130, .131); 3 6th cervical vertebrae (.132- .133), (1 USNM); 15 caudal vertebrae (.135- .143), (3 USNM), (3 UF); 3 articulated caudal vertebrae (.134a-c); 1 lumbar vertebra (.144); 1 thoracic vertebra (.145); 9 vertebrae (.146- .148), (3 USNM), (3 UF); 1 vertebra (.150); 1 sacral vertebra (1 USNM); 1 sacral vertebra and two associated caudal vertebra (1 UF); 1 partial hyoid process (.149); 2 proximal rib halves (.151, .152).

Remarks: The muskrat is by far the most common mammal from the Ardis local fauna. The relatively high number of muskrat remains from the site suggests that they may have been using the solution cavities as temporary shelters. Given that the deposit at the Ardis local fauna represents fluvial episodic events, these cavities may have provided excellent temporary shelters if muskrats retreated from their usual shelters onto higher ground during periodic flooding. This behavior has been observed in muskrats using multiple shelters in areas with seasonal fluctuations in water levels (Brooks 1985). In addition, pieces of fossil turtle shell collected from the site had gnaw marks of a large rodent, presumably muskrats, suggesting that feeding may have occurred in these cavities. It is unlikely that the turtle shells were "wash-ins," as no signs of weathering, water wear, or abrasive breakage were evident. There have been many reports of contemporary muskrats feeding upon turtles (Errington 1941, Doult et al. 1966, Parmalee 1989), but no reports of this have been recorded from the fossil record.

The muskrat is found throughout much of North America, including all of South Carolina. This is the most aquatic of the microtine rodents and is usually found in close proximity to fresh or brackish waters.

This is the first fossil record of this species from South Carolina.

*Neofiber alleni* - Round-tailed Muskrat (Florida Water Rat)

Material: 1 right M1 (.153); 1 fragmentary molar (.154).

Remarks: *N. alleni* is endemic to Florida and southernmost Georgia, and its northward limits may be maintained by aridity and cold temperatures (Frazier 1977). It is not currently sympatric with *O. zibethicus*.

The enamel above the jaw line on the partial molar appears to be chemically etched or corroded. This may be due to the ingestion of this specimen by a carnivore, at which point only the dorsal portion of the tooth would be exposed to stomach acids (Gary Morgan, Florida Museum of Natural History, personal communications). Separation of the molar from the dentary bone may have occurred during or after fossilization. This species is a good indicator of nearby bodies of permanent water; its diet consists mostly of aquatic vegetation. It builds its nest in areas such as open savannahs, mangroves, and in suitable stumps (Kurten and Anderson 1980).

This is the first fossil record of the round-tailed muskrat outside of Florida and Georgia.

*Synaptomys cooperi* - Southern Bog Lemming

Material: 1 right M1 (.155).

Remarks: The molar from the Ardis site compares favorably to recent specimens of this species. Separation of *Synaptomys cooperi* from *S. australis* is based on size, as *S. cooperi* is generally 35% smaller than *S. australis* (Simpson 1928, Olsen 1958). The occlusal length (2.2 mm) of the Ardis M1 referred to *S. cooperi* is comparable to the lowest range given by Guilday et al. (1977).

The southern bog lemming can be found in habitats that include grasslands, moist meadows, woodlands, thickets, weedy fields, and bogs (Webster et al. 1985).

*Synaptomys cooperi* does not occur in the State today; the nearest populations are found in the Piedmont and mountains of Virginia and North Carolina, respectively, extending north into Maryland, and westward into Kansas and Nebraska (Hall 1981). *S. cooperi* also occurs in the Great Dismal swamp and on the Coastal Plain of North Carolina (Clark et al. 1993).

This is the first fossil record of the southern bog lemming from South Carolina.

*Synaptomys australis* - Florida Bog Lemming

Material: 1 right M1 (.156).

Remarks: This species, though morphologically similar to *S. cooperi*, was distinguished by its significantly larger occlusal surface length of 3.4 mm than *S. cooperi* (Simpson 1928, Olsen 1958). Apparently this is the first sympatric occurrence of *S. cooperi* and *S. australis* in a fauna known to be contemporaneous. Both species were recovered from Ladds quarry, Georgia, but may have come from strata of two different ages in the deposit (Kurten and Anderson 1980).

There has been some debate over whether or not the extinct *S. australis* is a full species, represents a cline for greater body size, or a large subspecies of *S. cooperi*. Their sympatric occurrence in the Ardis Local Fauna suggests that they were distinct.

This is the first fossil record of this species from South Carolina.

*Microtus pennsylvanicus* - Meadow Vole

Material: 2 right dentaries one complete (.158) and the other containing only the m1 (.159); 2 left dentaries, one missing its proximal third and the m3 (1 USNM), and one fragment containing only the m1 (.160); 2 palatines, one with right M1 and M2 along with zygomatic arch (.161) and one with right M1 and the left M2 (.162).

Remarks: The meadow vole today inhabits a wide variety of habitats including upland grasslands, meadows, swamps, stream borders, salt marshes, and forests (Webster et al. 1985).

*M. pennsylvanicus* is commonly collected from Pleistocene sites in North America (Kurten and Anderson 1980), and now occurs in the Piedmont and in isolated populations near Charleston, South Carolina, and Cedar Key, Florida (Webster et al. 1985, Woods et al. 1982). *M. pennsylvanicus* does not currently occur in the vicinity of the Ardis fauna.

This is the first fossil record of this species from South Carolina.

*Microtus pinetorum* - Woodland Vole

Material: 1 right dentary with a complete dentition (.163); 1 right m1 (.164); 2 left dentaries, one missing proximal third and m3 (.165), one missing proximal third and m2 and m3 (.166); 1 maxilla with left M1 and the right M3 (.167).

Remarks: Identification was based on criteria established by Martin and Webb (1974) and Martin (1991). The woodland vole typically

inhabits woodland and old-field habitats and is well known for building extensive shallow tunnels (Webster et al. 1985). *M. pinetorum* can be found throughout South Carolina and is common in the pine forests of the South and in eastern deciduous forests (Kurten and Anderson 1980).

This is the first fossil record of this species from South Carolina.

Subfamily Sigmodontinae

*Oryzomys palustris*. - Marsh Rice Rat

Material: 1 left dentary lacking dentition (.175).

Remarks: Identification was based on several features, including double rooted molars, mental foramen at base of M1, diastema short and robust (compared to *Peromyscus*), anterior root of M1 ventral and offset from other roots, foramen next to M3 much larger than *Peromyscus*, and over-all size correlation to *Oryzomys*, and direct comparisons to recent specimens.

The marsh rice rat inhabits marshlands, meadows, and wet grasslands on the Coastal Plain of South Carolina and has been recorded along a mountain stream in South Carolina (Webster et al. 1985).

This specimen represents the first fossil record of this species from the State.

*Peromyscus* sp.

Material: 1 right dentary containing only the incisor (.168).

Remarks: Identification was based on the alveolar length of the tooth row, and similarities in morphology and size when compared to recent *Peromyscus*. The tooth row is longer than that of *Reithrodontomys*.

Several species of *Peromyscus* inhabit the northwestern portion of South Carolina. *P. gossypinus*, the largest member of this genus inhabiting the State, is the only species of *Peromyscus* that can be found today in the area of the Ardis site. The robustness of the fossil specimen suggests this species, but, given the presence of numerous extralimital species in the fauna, it is not possible to assign the fossil to a particular species of *Peromyscus* with any certainty.

*Neotoma floridana* - Eastern Woodrat

Material: 1 left M1 (.169); 1 right innominate bone (.170).

Remarks: Woodrats are notorious collectors of natural history objects. Apparent rarity of this species in the Ardis local fauna notwith-



standing, activities of this species may explain some of the more unusual occurrences of other vertebrate species in the solution cavities. The three-rooted M1 compares favorably in morphology and size (anterior-posterior length of M1 = 3.52 mm) to recent material. *N. floridana* is the only species of woodrat found in the southeastern United States.

This represents the first fossil record of this species from South Carolina.

#### Family Hydrochaeridae

Material: 1 fragment of the posterior lamina of the M3 (.184).

Remarks: Identification to family was based on direct comparison to fossil and recent specimens. However, the fragmentary nature of the specimen precludes identification to genus or species.

The extremely thin enamel and the particular angle of the fragment are diagnostic and cannot belong to any other taxon.

One living genus of capybara (*Hydrochaeris*) occurs in tropical habitats in Central and South America and is semiaquatic, commonly found along the edges of streams and the borders of marshes (Kurten and Anderson 1980). The presence of this tropical family in the fossil record was first established for South Carolina by Roth and Laerm (1980).

#### Order Lagomorpha

##### Family Leporidae

##### *Sylvilagus palustris* - Marsh Rabbit

Material: 4 right dentaries (.185-.187), (1 UF); 3 left dentaries (.188-.189), (1 USNM); 1 isolated p3 (.190).

Remarks: Identification was based on the presence of multiple anterior reentrants on the third premolar.

The marsh rabbit is a good swimmer and can be found in wetlands areas such as marshes, flood plains, and hummocks, and its modern distribution ranges from southeastern Virginia along the Atlantic Coastal Plain into Florida (Webster et al. 1985). *S. palustris* probably occurs in the immediate vicinity of the Ardis site. It has been recorded from many Pleistocene sites in Florida (Webb 1974, Kurten and Anderson 1980), and *Sylvilagus* sp. was identified from Edisto Island, South Carolina (Roth and Laerm 1980).

This represents the first fossil material identified as this species from South Carolina.



*Sylvilagus floridanus* - Eastern Cottontail

Material: 2 left (.191, .192) and 1 right dentary (1 USNM).

Remarks: Remains were identified by complete absence or presence of a single anterior reentrant on the p3.

This species is distributed from southern Canada south to Argentina (Kurten and Anderson 1980). The eastern cottontail typically inhabits areas with a mixture of herbaceous and shrubby plants in a disturbed environment at some stage of successional transition that occur in and among a variety of habitats (Webster et al. 1985). The eastern cottontail occurs in the area of the Ardis site today.

This is the first fossil record of this species reported from South Carolina.

*Sylvilagus* sp.

Material: 2 right distal femora fragments (.213, .214); 3 left partial femora (.215, .216), (USNM); 1 right humerus (.217); 1 left distal half of a humerus (.218); 1 proximal end of a humerus (.226); 1 right partial scapula (.219); 2 distal and 1 proximal tibio-fibia ends (3 USNM); 1 left partial radius (.220); 1 ulna proximal end (.221); 4 left partial innominate bones (.222, .223), (2 USNM); 3 left calcanea (.224), (2 UF); 3 right calcanea (.225), (2 USNM).

Remarks: All of the leporid postcranial elements from the Ardis local fauna represent this genus, but we are unable to assign these elements to a particular species in this genus.

## DISCUSSION

## PALEOECOLOGY AND PALEOCLIMATE

The Ardis local fauna is one of only a handful of Rancholabrean sites reported from the Atlantic Coastal Plain north of Florida, and is the only C14 dated fauna from South Carolina. It was deposited during the full glacial phase of the Wisconsin. This interval is poorly represented in the fossil record, with New Trout Cave, West Virginia (Grady and Garton 1982) and Bakers Bluff, Tennessee (Guilday et al. 1978) being the only other fossil sites in the southeastern United States known to be temporally similar.

Two biases must be considered which may have skewed types and frequency of remains recovered from the Ardis site: 1) collection bias; a disproportional amount of the larger "easier to see" material was collected. Comparatively little of the fossiliferous sediments was screen-washed to retrieve the smaller material otherwise easily missed

and 2) depositional and behavioral biases; the smaller taxa, particularly those that used this site as a shelter or in hunting, should be represented in disproportionately higher numbers when compared to the megafauna. Behavioral and environmental factors influence the occurrence of the smaller taxa which could easily enter the cavities from the surface. Furthermore, some taxa may have been concentrated in the stomachs of predators who were subsequently entombed in the cavities. The above-mentioned factors, excluding predation, but including other taphonomic factors, especially the size-restrictive nature of the cavity openings, would govern the lower frequency of the larger megafauna occurrence in the cavities. Therefore, the species composition most likely is not proportional to its true occurrence in this particular Pleistocene community.

Relatively large faunal diversity may give a reasonably reliable picture of the surrounding habitat (Guilday 1962). The taxa of the Ardis local fauna represent a diversity of ecological niches including semi-aquatic forms (*Castor*, *Lontra*, *Ondatra*, *Tapirus*, and *Mustela vison*), arboreal forms (*Glaucomys volans*, *Sciurus carolinensis*), marsh and meadow inhabitants (*Synaptomys*, *Microtus*, *Oryzomys*), grassland or prairie forest transition inhabitant (*Spermophilus tridecemlineatus*), and the large grazers and browsers (*Palaeolama*, *Bison*, *Equus*, *Odocoileus*, *Megalonyx*, *Mammut*, and *Mammuthus*), suggesting that the Ardis fauna sampled an ecological mosaic of community types. The depositional features and fauna suggest a composite conifer and hardwood forest, interspersed or bordered by a grassland/meadow, possibly giving way in low-lying areas to a marsh or bog, with a permanent nearby stream or river.

Hypothesized changes in vegetation during the late Pleistocene (Dreimanis 1968), with climatic conditions unlike any experienced in North America today (COHMAP Members 1988), are reflected in the extralimital tropical to boreal species found in the Ardis fauna.

Of the 43 mammalian species collected from the site, 27 are extant, 21 still occurring in the area today. Of the six extant extralimital taxa, four have more northern affinities, one a midwestern affinity, whereas only one has a range well south of the Ardis site. Of the 16 extinct taxa, five have affinities considerably south and west of the Ardis locality (Kurten and Anderson 1980, Martin 1978).

The Ardis mammal fauna exhibits a mixture of southern, western, and northern forms, resulting from the radiation and convergence onto the lower Atlantic Coastal Plain of taxa migrating along the Gulf Coast corridor (Webb 1974) and taxa migrating from the north-west Appalachian Mountains region. It is plausible that *Spermophilus tridecemlineatus* may have entered South Carolina from a northern

route instead of along the Gulf Coast corridor, as attributed to the fossil remains from the Haile 14A fauna (Webb 1974). Fossil localities reporting *S. tridecemlineatus* (Kurten and Anderson 1980) and other fossils collected from the Ardis site, in particular a portion of the turtle fauna (Bentley and Knight, submitted), strongly suggests the existence of a northern corridor(s) onto the Atlantic Coastal Plain. This would be a logical pathway for those glacially displaced species of the Northeast found at the Ardis site.

*Blarina brevicauda*, *Microtus pennsylvanicus*, and *Synaptomys cooperi* are interpreted as "boreal" or "cool climate" components of the Ardis fauna, based on modern distribution and habitat orientation (Hoffman and Jones 1970, Graham 1976, Webster et al. 1985). *Neofiber alleni* is considered a sub-tropical or "warm climate" species based on modern distribution and fossil records (Martin and Webb 1974, Frazier 1977, Kurten and Anderson 1980, Holman 1985).

Those extinct species collected from the Ardis fauna with extant genera or families primarily tropical to sub-tropical in distribution include: *Tremarctos floridanus*, *Palaeolama mirifica*, *Conepatus robustus*, *Tapirus veroensis*, and the family Hydrochoeridae. *Holmesina septentrionalis* has also been interpreted as indicating a mild climate (Kurten and Anderson 1980).

Generalization of ecological needs of an extinct species based on the needs of extant relatives cannot always be considered reliable. However, when several such groups are geologically recent, are in a single locality, and represent a short depositional time interval, as at the Ardis site, these assumptions become more credible.

The modern Coastal Plain fauna of South Carolina has six species of microtines, three species of shrews, and two mole species (Webster et al. 1985). Fossil remains of both mole species and two of the three shrew species were collected from the Ardis fauna, along with eight microtine species. Greater microtine densities in late Pleistocene faunas have been correlated with reduced temperature and moisture gradients (Graham 1976). This is also true for shrew species (Graham 1976), but we did not observe it in the Ardis fauna. The reduction in the number of shrew species at the Ardis site is probably a result of collection bias and not a true reflection of the shrew populations.

Martin (1968) suggested that the distribution of *M. pennsylvanicus* is limited mostly by warmer temperatures and drier summers, but also by the presence of *Sigmodon hispidus*, which was inexplicably absent from the Ardis fauna. The mean July temperature for the southern boundary of *M. pennsylvanicus* is  $23.9 \pm 1.1$  C (Martin 1968), and

the two species occur sympatrically in areas where the mean July temperature is near 26.7 C (Martin 1968). Today, *S. hispidus* is common throughout South Carolina, but *M. pennsylvanicus* is present only in the extreme western Piedmont and in a small relict population near Charleston, South Carolina (Webster et al. 1985). Data from Charleston, South Carolina, over the past 75 years yielded a July daytime mean of 31.1 C and a minimum daily mean of 23.9 C (Pearce and Smith 1984). Vegetational data for the late Wisconsin full glaciation, taken from White Pond in South Carolina (Watts 1980), suggested a 7 C to 20 C decrease in July temperatures compared to present, and possibly a marginal reduction in precipitation. The presence of *M. pennsylvanicus* in the Ardis fauna and the absence of *S. hispidus* may indicate slightly drier conditions and temperatures below the mean summer temperature experienced today.

It has been postulated that mammals in the late Pleistocene reacted to environmental changes based on their own tolerance limits and not as a "community unit" (Graham 1976, 1979). This accounts for northern species pushed south by glaciation and then integrating with the existing biota. Furthermore, southern species also were integrated into the resident community as cooler summers and warmer winters prevailed, producing the "disharmonious fauna" collected from the Ardis fauna.

In general, the mammalian composition of the Ardis fauna, containing distinctly southern, northern, and western extralimital forms, reflects a climate more equitable than present. The less severe climatic gradients would facilitate the sympatric occurrence of species now ecologically incompatible. The Ardis local fauna coincides well with other late Pleistocene fossil localities reporting disharmonious faunas with similar temporal and topographical settings. This suggests that the late Pleistocene in the southeastern United States was climatically more equitable and ecologically more diverse prior to the dramatic shift towards a modern assemblage, approximately 10,000 to 11,000 y.b.p. (Lundelius et al. 1983).

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## APPENDIX I

### TAXA AND MINIMUM NUMBER OF INDIVIDUALS

Taxa	Minimum Number of Individuals
<i>Didelphis virginiana</i> *	6
† <i>Dasypus bellus</i>	1
† <i>Holmesina septentrionalis</i> (S)	1
† <i>Megalonyx jeffersoni</i>	1
<i>Sorex</i> sp. cf. <i>S. longirostris</i> *	1
<i>Blarina brevicauda</i> *(N)	3
<i>Scalopus aquaticus</i> *	11
<i>Condylura cristata</i> *	2
<i>Urocyon</i> cf. <i>U. cinereoargenteus</i>	1

† <i>Canis dirus</i>	1
†cf. <i>Smilodon fatalis</i>	1
<i>Lynx rufus</i> *	1
<i>Lontra canadensis</i> *	1
<i>Spilogale putorius</i> *(N)	1
<i>Mephitis mephitis</i> *	1
† <i>Conepatus robustus</i> *(S)	1
<i>Mustela vison</i> *	5
<i>Procyon lotor</i>	2
† <i>Tremarctos floridanus</i> (S)	1
† <i>Mammut americanum</i>	1
† <i>Mammuthus columbi</i>	2
† <i>Equus</i> cf. <i>E. complicatus</i>	2
† <i>Tapirus veroensis</i>	2
† <i>Mylohyus nasutus</i>	1
† <i>Palaeolama mirifica</i> (S)	1
<i>Odocoileus virginianus</i>	2
† <i>Bison antiquus</i>	1
<i>Glaucmys volans</i> *	1
<i>Sciurus carolinensis</i> *	1
<i>Spermophilus tridecemlineatus</i> *(MW)	1
<i>Castor canadensis</i>	1
<i>Ondatra zibethicus</i> *	13
<i>Neofiber alleni</i> *(S)	1
<i>Synaptomys cooperi</i> *(N)	1
† <i>Synaptomys australis</i> *(S)	1
<i>Microtus pennsylvanicus</i> *(N)	3
<i>Microtus pinetorum</i> *	3
<i>Oryzomys palustris</i> *	1
<i>Peromyscus</i> sp.*	1
<i>Neotoma floridana</i> *	1
Hydrochoeridae(S)	1
<i>Sylvilagus palustris</i> *	4
<i>Sylvilagus floridanus</i> *	2
Faunal list = 43 species	Total 89

\* = first fossil record from South Carolina

(N) = extralimital northern (S) = extralimital southern

(MW) = extralimital mid-western

† = Extinct taxa